

Effects of Habitat Quality on the Number of Alloparents and Nest Provisioning Rates in a Cooperatively Breeding Tropical Passerine

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Phetprakhai Wonkson, Tommaso Savini, and George A. Gale (2012) Effects of habitat quality on the number of alloparents and nest provisioning rates in a cooperatively breeding tropical passerine. *Zoological Studies* 51(8): 1464-1474. Habitat quality is likely to impact group size, provisioning behavior, and nesting success of cooperatively breeding birds; however, predicting the direction of these effects is particularly challenging. We investigated the influence of habitat quality on the number of alloparents in breeding groups and whether the presence or the number of alloparents influenced nest survival, provisioning rates, and individual breeder workloads in the Puff-throated Bulbul (*Alophoixus pallidus*), a tropical understory passerine. We used arthropod biomass as a proxy for habitat quality of 17 territories. We also analyzed data from 143 nests from 41 breeding groups during 3 breeding seasons to assess effects of alloparents on reproductive success. Habitat quality was not significantly correlated with the number of alloparents per group ($p = 0.07$), the number of fledgling produced ($p = 0.08$), or the provisioning rate ($p = 0.99$). The number of fledglings produced was also not significantly correlated with the number of alloparents ($p = 0.71$). Overall provisioning rates were marginally higher for groups with no alloparents compared to groups with alloparents ($p = 0.055$), but provisioning rates of breeders significantly declined with increases in alloparent numbers ($p < 0.05$). The lack of simple habitat effects on the number of alloparents may have been due to a complex suite of factors affecting both the production and dispersal of offspring and the recruitment of unrelated alloparents. The lack of a correlation between nesting success and alloparent numbers may have been due to the inability of adult birds to dissuade most predators in this system. <http://zoolstud.sinica.edu.tw/Journals/51.8/1464.pdf>

Key words: *Alophoixus pallidus*, Provisioning, Puff-throated Bulbul, Variable social structure, Alloparents.

One of the important hypotheses explaining cooperative breeding in birds focuses on territory quality and the lack of breeding opportunities due to habitat saturation (Emlen 1982, Komdeur et al. 2008). Stacey and Ligon's (1987 1991) "benefits of philopatry" hypothesis predicts that young birds will stay on high-quality territories, because they gain direct benefits, including increased survivorship, and indirect benefits derived from helping, which exceed the fitness they expect to gain by dispersing to breed independently on available lower-quality territories. From the breeder's point of view, alloparents (defined here following Wilson (1975) as individuals providing parent-like care

of young produced by individuals other than the caregiver) can reduce provisioning workloads for the breeding female and male (Eden 1987), reduce mortality for both breeders and helpers (Russell and Rowley 1988, McGowan et al. 2003), increase feeding rates for nestlings (Covas and de Plessis 2005), and increase reproductive success of the breeders (Komdeur 1994, Canestrari et al. 2008). For species which have groups containing alloparents who are offspring from previous broods, the presence of these birds may be an indicator that the female produced more young in the given year compared to females with no alloparents present (i.e., suggesting that none of her offspring

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survived) (Russell and Rowley 2000). Conversely, in other species, pairs may only accept unrelated alloparents to assist in raising offspring in cases where territory quality is particularly poor (Reyer 1980). In such species, these unrelated helpers benefit by raising offspring of others in that they gain potential access to mates and therefore have at least some chance of producing offspring. For example, the female alloparents of the White-throated Magpie Jay (*Calocitta formosa*) produced 16% of the young in a population (Berg 2005). Thus, mating systems may be highly dependent on habitat quality, which can be assessed using a variety of indices. Furthermore, given these potential responses to good and poor habitats, predicting how territory quality will affect group size in a species which has potentially both related and unrelated alloparents is likely to be particularly challenging.

This study focused on the cooperatively breeding Puff-throated Bulbul *Alophoixus pallidus* (family Pycnonotidae). Approximately 2/3 of *A. pallidus* groups consist of breeding pairs together with alloparents, while the remaining 1/3 exist only as pairs (Sankamethawee et al. 2009). Although the proportions are currently unknown, alloparents can be offspring from previous nesting attempts or unrelated adult birds (Pierce et al. 2007, Sankamethawee et al. 2009).

While fruit comprises 50%-85% of the adult diet depending on the season (Khamcha et al. 2012), previous work on the Puff-throated Bulbul suggested that fruit availability was not correlated with home range or group size (Tanasarnpaiboon 2008). Conversely, arthropods comprise at least 68% of the nestling Puff-throated Bulbul diet (fruit = 4% and unidentified = 28%) (Wonkson unpubl. data); thus, we focused on arthropods as an index of territory quality following Smith and Shugart (1987) and Ridley et al. (2003).

We examined the overall pattern of whether habitat quality influences the number of alloparents, and we also studied the influence of alloparents on nesting success and parental care. We addressed 3 main questions: 1) Is the number of alloparents related to habitat quality?; 2) How does habitat quality affect the reproductive success of breeders with and without alloparents?; and 3) How does the presence of alloparents influence parental care of primary breeders?

MATERIALS AND METHODS

Study area

We conducted the study during 2007-2009 on the 30-ha Mo-Singto Long-term Biodiversity Research plot (Fig. 1) at Khao Yai National Park, northeastern Thailand (14°26'N, 101°22'E), at elevations of 723-817 m. The plot is classified as a mature, seasonally wet evergreen forest where every tree with a diameter breast height (DBH) of ≥ 1 cm has been mapped, tagged, and identified (for plot details see Brockelman et al. 2011). The canopy layer is approximately 30-35 m tall; the understory layer is dominated by *Polyathia evecta* (3-5 m) (Brockelman 1998, Lertpanich and Brockelman 2003). The average annual rainfall is 2504 mm (2006-2009) which mostly falls between May and Oct.; the dry season occurs from Nov. to Feb. Average humidity is 86.6%, and average temperature is 22.2°C.

Study species

The Puff-throated Bulbul is omnivorous, with adults consuming 50%-85% fruit and 15%-50% arthropods (Sankamethawee et al. 2011, Khamcha et al. 2012). It is found in evergreen forests of Cambodia, China, Laos, Myanmar, Thailand, and Vietnam (BirdLife International 2009). In Thailand, the species is a common resident in broadleaf evergreen forests up to 1450 m in central and northeastern regions (Lekagul and Round 1991, Robson 2000). A recent study found that they were one of the most abundant birds on the Mo-Singto plot (3.4 birds/ha) (Gale et al. 2009). Puff-throated Bubluls build open-cup nests between Feb. and July, which are situated 0.5-15 m above the ground (Pierce et al. 2004). Only breeding females contribute to nest building, incubation, and brooding, while both males and females provision nestlings and fledglings (Sankamethawee et al. 2009). Adult Puff-throated Bubluls in the study area were caught using mist-nets and ringed with unique color combinations of 1 numbered aluminum ring and 2 or 3 plastic color rings. Nestlings were ringed at an age of 8 or 9 d after hatching. Territorial boundaries of each group were mapped from encounter locations (Sankamethawee et al. 2009). These boundaries fluctuate relatively little within a year (Khamcha et al. 2012). Twenty groups of Puff-throated Bulbul were selected to assess habitat quality in 2009. Five groups were comprised of 2 individual adult

birds (2V, AE, AX, HA, and RU), another 8 groups had 3 adults (AS, DA, FN, FU, L, MP, NU, and X), and the remaining 7 groups had 4-7 individuals (AF, CAMP, F, GAP, GH, RF, and S) (Fig. 1).

Nest observations

We searched for nests of Puff-throated Bulbul during the breeding season, Feb.-July. Nests from every group which lived in and adjacent to the study plot were used to assess nest success, which in this case was defined as the number of fledgling produced. Nests below 7 m high were checked every 2-3 d until the nest had failed or successfully fledged at least 1 young. During the nestling stage, nests were observed using a 20-60x zoom telescope and 8 × 30-mm binoculars, from a camouflage blind at least 10 m (and typically 15-20 m) from the nest to avoid disturbing nesting activities. Each nest was observed for at least 4 h

during the nestling stage in both the morning and afternoon. We also observed provisioning for at least 2 h in the 1st week after fledging. During the observations, notes were taken on every feeding bout, the brooding intensity, and activities of adults perching on or near the nest (< 15 cm). Ring combinations of all individuals visiting nests were recorded to determine individual workloads. Types of food delivered were identified as plant or animal, and where possible, animal food was classified to at least the order level.

Arthropod sampling

The study area was divided into 20 × 20-m quadrates (Fig. 1). For each bulbul group we conducted monthly arthropod sampling during Jan.-Dec. 2009 within the territories of each of the 20 groups (Fig. 1). Due to logistical constraints, traps were located at only 1 random location within

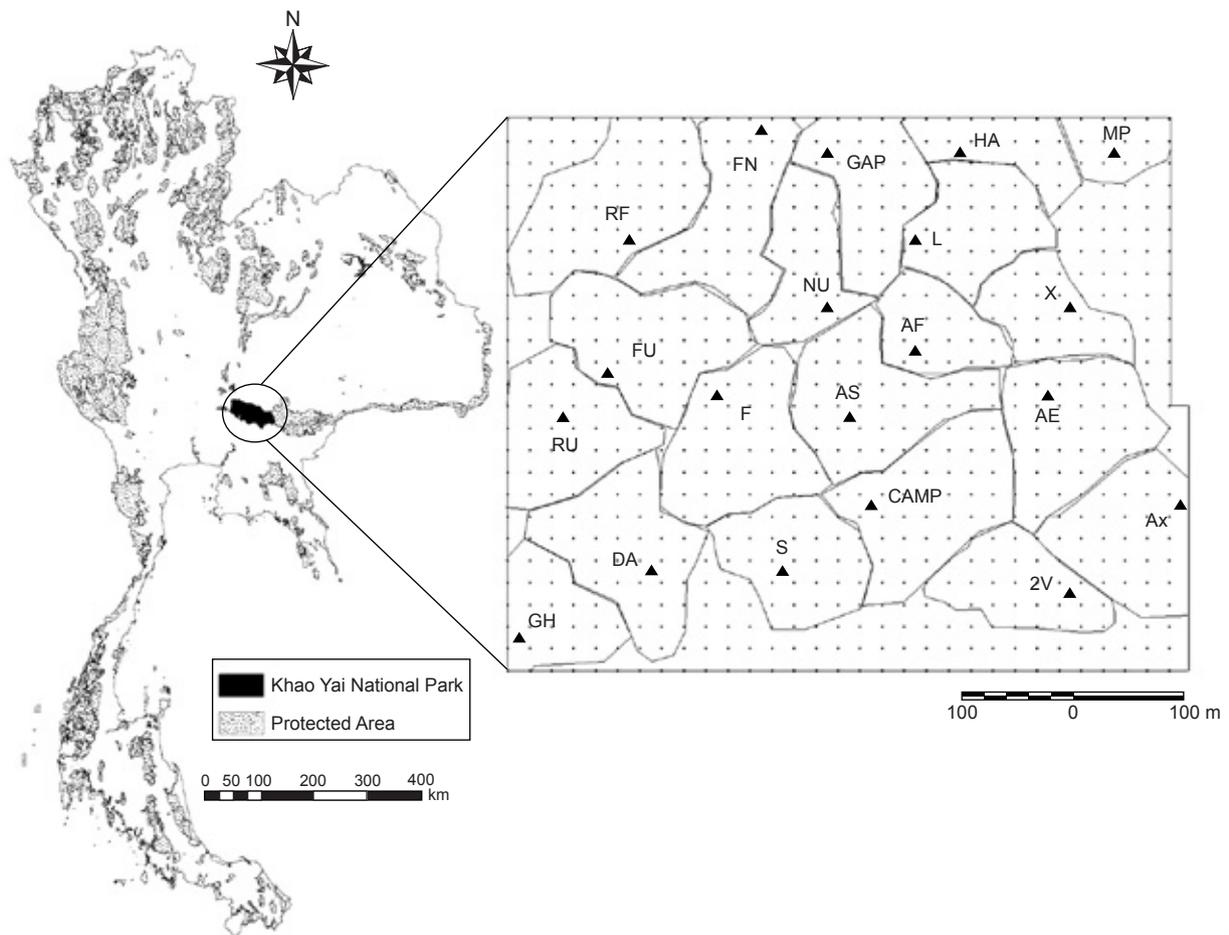


Fig. 1. Map of the Mo-Singto Long-term Biodiversity Research plot. Each polygon represents a Puff-throated Bulbul group territory (based on Sankamethawee 2009). Solid triangles indicate arthropod trap locations.

each selected territory. We conducted standard aerial malaise trapping for flying insects 1 wk/mo in each territory. Traps were placed at varying heights of 7-17 m based on the availability of branches on which to hang the traps near the selected sampling points. We emptied all traps after 7 d. Arthropod samples were preserved in 70% ethyl-alcohol before identification, and then they were dried at 80°C for 48 h to obtain the biomass.

As portions of the 20 focal territories were outside the study plot, we only used groups for which we had habitat data for > 70% of a given territory area to analyze habitat quality in relation to group size ($n = 17$ groups). Due to the limited sampling per territory, we predicted arthropod index values for all the other 20 × 20-m quadrates which had no arthropod data using linear regression models. This index was then used as an index of territory quality for each of these 17 groups. The independent data for the models included tree data from the Mo-Singto tree database (Brockelman et al. 2011), which is comprised of the basal area of large trees, (DBH > 10 cm), the basal area of small trees, (DBH ≥ 110 cm), species richness of large trees, and species richness of small trees. Studies showed that vegetation variables, including tree species richness, tree basal area, and tree density, are related to the richness and abundance of at least selected arthropod species (Grove 2002, Sperber et al. 2004). We used the Akaike information criterion corrected for small sample sizes (AIC_c) to find the best models for predicting arthropod dry weight obtained from the malaise

traps.

Although the null model was the top model for predicting arthropod biomass (Table 1) which suggested that our vegetation variables were only moderate predictors, we only used vegetation variables and did not use the null model to develop the arthropod dry-weight index for the final analyses because (1) traps were often located at the edges of territories rather than at their centers due to randomized placement (Fig. 1), (2) a spatial autocorrelation analysis (below) indicated that individual malaise traps were probably not representative of individual territories, and (3) our literature review above indicated that the vegetation parameters we used are known to be correlated with arthropod biomass. Model averaging was based on all vegetation models that contributed at least 90% to the total relative model weights (Burnham and Anderson 1998, Bolker 2008). We then estimated an index of predicted arthropod dry weight for each territory based on this regression (Table 2).

In a preliminary analysis, we tested for non-linear effects by constructing generalized linear models (GLMs) of habitat quality (average arthropod dry weight) using quadratic or polynomial predictors of the number of alloparents. We then visually inspected the relationship between habitat quality and number of alloparents. Models with non-linear terms were a worse fit to the data, based on the AIC_c , and visual inspection of the data revealed no non-linear patterns. Therefore, we used linear models to analyze our bulbul and arthropod index data.

Table 1. Models showing the relationship between vegetation variables (including the null model) and arthropod dry weight obtained from malaise traps. Variables are coded as follows: BL, basal area of large trees; BS, basal area of small trees; TL, number of species of large trees; and TS, number of species of small trees. For each model, the number of parameters (K), corrected Akaike information criterion (AIC_c), differences in AIC_c scores relative to the top-ranked model (ΔAIC_c), model weight (w_i), and adjusted r -squared (R^2) values are shown

Model	K	AIC_c	ΔAIC_c	w_i	R^2
Arthropod dry weight from malaise traps					
1. $y = \beta_0$	1	49.82	0.00	0.28	-
1. $y = \beta_0 + \beta_1(BL) + \beta_2(BS) + \beta_3(TS)$	4	51.02	1.19	0.16	0.21
2. $y = \beta_0 + \beta_1(BL)$	2	51.28	1.46	0.14	0.01
3. $y = \beta_0 + \beta_1(BS)$	2	51.29	1.47	0.14	0.01
4. $y = \beta_0 + \beta_1(TS)$	2	51.66	1.84	0.11	-0.006
5. $y = \beta_0 + \beta_1(TL)$	2	52.61	2.75	0.07	-0.05
6. $y = \beta_0 + \beta_1(BL) + \beta_2(BS)$	3	53.47	3.64	0.05	0.005
8. $y = \beta_0 + \beta_1(BL) + \beta_2(BS) + \beta_3(TL) + \beta_4(TS)$	5	54.25	4.42	0.03	0.21

We examined the biomass data for spatial autocorrelations among traps using Moran's I with PAST software (Hammer et al. 2001). This was used to assess whether biomass from traps nearer to each other were more similar (or different) than expected by chance compared to those further away. This allowed us to assess spatial variations in biomass at different scales across the plot (*sensu* Lichstein et al. 2002). Despite large variations in arthropod biomass among traps (with a coefficient of variation of 42.8%), there was no significant spatial autocorrelation at the average distances tested (90, 233, and 439 m; $p > 0.12$, Moran's I = ~ 0 for all 3 distances tested). This suggested that factors affecting trap biomass probably occurred at scales of $\ll 90$ m, and that arthropod samples were likely to vary substantially across a territory (with an average territory area of 1.5 ha, Sankamethawee et al. 2010), and therefore single trap locations were highly unlikely to be representative of individual group territories. Because of the relatively wide spacing among traps and the small sample, we were unable to test for spatial structure at distances of < 90 m.

Data analysis

As parts of the 20 focal territories were outside the study plot, we only used groups for which we had habitat data for $> 70\%$ of a given territory area to analyze the habitat quality in relation to the group size ($n = 17$ groups). We used GLMs (Poisson regression) to test the effect of habitat quality (the arthropod index noted above) on the number of alloparents and fledglings

produced in 2009, as this was the only year in which arthropod data were collected. We tested the relationship between the provisioning rate and habitat quality using linear regression models, as we only had provisioning data for 9 nests from 7 territories observed during 2009.

To assess nest success in relation to group size, we used data from 143 nests (from 43 groups which lived in or adjacent to the plot) from 3 yr (2007-2009) of the study. Nests were visited approximately every 3 d on average, and success or failure could generally be determined by the timing of when nestlings disappeared. We used the number of fledglings produced as an index of nest success (Conner et al. 2004) and examined the effect of the number of alloparents on the number of fledglings produced using generalized linear mixed models (GLMMs; with the group identity as a random effect). Group location in general did not change from year to year, but group compositions often did. Previous work on the plot suggested that predation was the greatest source of nest failure (Pierce and Pobprasert 2007).

During the 3 breeding seasons, we observed 28 nests during the nestling stage and 15 broods during the fledgling stage to assess provisioning rates and food items brought to the nestlings or fledglings. We tested the provisioning rates between the time of day (morning vs. afternoon) and provisioning rates among different years (2007-2009) and found no significant difference, and thus data were pooled for the analyses. We compared the total group provisioning rate among groups with different numbers of alloparents. For

Table 2. Models used to derive the arthropod biomass index from malaise traps tested for this study. The index was derived without the null model ($y = \beta_0$) shown in table 1. Variables are coded as described in the legend to table 1. For each model, the number of parameters (K), corrected Akaike information criterion (AIC_c), differences in AICc scores relative to the top-ranked model (Δ AIC_c), model weight (w_i), and adjusted r-squared (R^2) values are shown

Model	K	AIC _c	Δ AIC _c	w_i	R^2
Arthropod dry weight from malaise traps					
1. $y = \beta_0 + \beta_1(\text{BS})$	2	50.55	0.00	0.23	0.06
2. $y = \beta_0 + \beta_1(\text{BL})$	2	50.60	0.05	0.23	0.06
3. $y = \beta_0 + \beta_1(\text{TS})$	2	50.90	0.35	0.20	0.05
4. $y = \beta_0 + \beta_1(\text{TL})$	2	51.83	1.28	0.12	0.003
5. $y = \beta_0 + \beta_1(\text{BL}) + \beta_2(\text{BS}) + \beta_3(\text{TL}) + \beta_4(\text{TS})$	5	52.48	1.94	0.09	0.36
6. $y = \beta_0 + \beta_1(\text{BL}) + \beta_2(\text{BS})$	3	52.50	1.95	0.09	0.10
7. $y = \beta_0 + \beta_1(\text{BL}) + \beta_2(\text{BS}) + \beta_3(\text{TS})$	4	54.76	4.21	0.03	0.05
8. $y = \beta_0 + \beta_1(\text{BL}) + \beta_2(\text{BS}) + \beta_3(\text{TL})$	4	55.65	5.10	0.02	0.10

the analysis of provisioning, we divided the bulbul groups into 3 categories: pairs, 3 individuals, and 4-7 individuals. We also compared provisioning rates by adult categories (i.e., breeding female, breeding male, and alloparents) using a one-way analysis of variance (ANOVA). All of the analyses were conducted using R software (R Development Core Team 2010).

RESULTS

Habitat quality, number of alloparents, nesting success, and provisioning rates

From the arthropod sampling, we found 13 orders of insects and 1 order of spider (class Arachnida; order Araneae). Habitat quality of territories (i.e., the average predicted dry weight of arthropods from malaise traps) was not significantly correlated with the number of alloparents ($p = 0.079$) ($AIC_c = 58.51$ for the null model vs. 57.35 for the alloparent model), although it was suggestive of a modest effect whereby more alloparents were predicted at sites with a lower arthropod index. In 2009, only 5 of the 17 focal groups successfully fledged young. The number of fledglings produced was not significantly related to habitat quality ($p = 0.083$) ($AIC_c = 53.56$ for the null model vs. 52.42 for the fledgling model). This was also perhaps suggestive of a modest effect whereby territories with lower arthropod values actually produced more fledglings, but this was largely based on only 5 data points. Provisioning rates of 9 nests (within 7 territories) were not significantly related to habitat quality ($p = 0.59$) ($AIC_c = 6.78$ for the null model vs. 8.78 for the provisioning model) (Fig. 2), thus there was no evidence to suggest that higher or lower provisioning rates at a given nest were associated with greater or lower arthropod availability.

Effect of the number of alloparents on nesting success

There were 15 groups of 2 individual birds (no alloparents) (36.6%), 11 groups with 3 individual birds (1 alloparent) (26.8%), and 15 groups that contained 4-7 birds (2-5 alloparents) (36.6%). The number of fledglings produced based on 3 yr of data ($n = 143$ nests) was not significantly related to the number of alloparents ($p = 0.71$).

Effect of the number of alloparents on provisioning rates

We observed 35 nests; 28 nests were observed during the nestling stage (7 nests in 2007, 11 nests in 2008, and 10 nests in 2009).

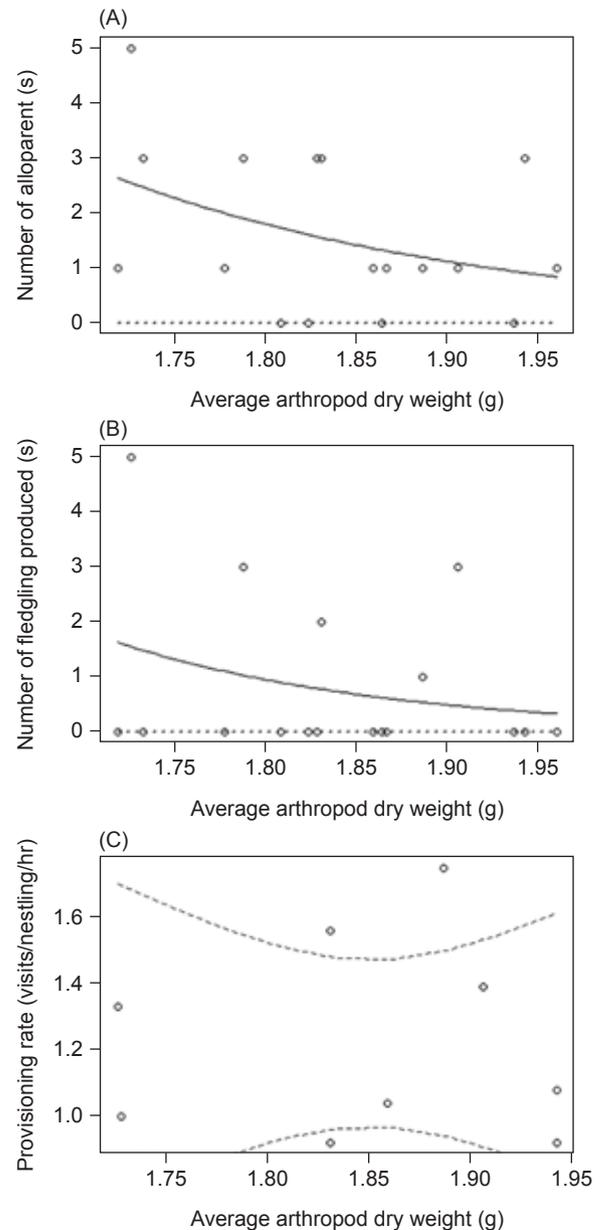


Fig. 2. An index of territory quality (average arthropod dry weight in grams obtained from malaise traps derived from regression models (see Table 1)) in relation to: (A) the number of alloparents in a group ($p = 0.079$, $n = 17$), (B) the number of fledglings produced ($p = 0.083$, $n = 17$), and (C) provisioning rates (visits/nestling/h) ($p = 0.59$, $n = 9$). Dashed lines indicate the 95% confidence intervals. For A and B, the upper confidence limits are out of range (~ 18).

Fifteen nests reached the fledgling stage (1 nest in 2007, 4 nests in 2008, and 10 nests in 2009). The overall provisioning rate during the nestling stage was 1.34 ± 0.4 visits/nestling/h ($n = 28$), and it was 3.43 ± 1.01 visits/nestling/h ($n = 15$) during the fledgling stage. The overall provisioning rate during the nestling stage of groups with no alloparents was marginally significantly greater than groups with 1 or more alloparent (ANOVA $F_{2,27} = 3.287$, $p = 0.055$; Table 3). Due to the small sample of nests during the fledgling stage (no alloparents $n = 2$, 1 alloparent $n = 3$, and 2-5 alloparents $n = 10$), we were unable to test for differences. The median ratio of identified arthropods to fruit items delivered to nestlings was $> 20:1$ and did not significantly differ among groups with different numbers of alloparents

(ANOVA $F_{2,32} = 0.537$, $p = 0.59$).

Provisioning rates by adults of different breeding statuses

Provisioning rates during the nestling stage by breeding females were significantly greater than those of breeding males and alloparents. Provisioning rates of breeding males and alloparents did not differ. During the fledgling stage, breeding females also had the highest provisioning rates, which were significantly greater than those of the alloparents. However, there was no difference in the provisioning rates between breeding females and breeding males, or between breeding males and alloparents (Fig. 3).

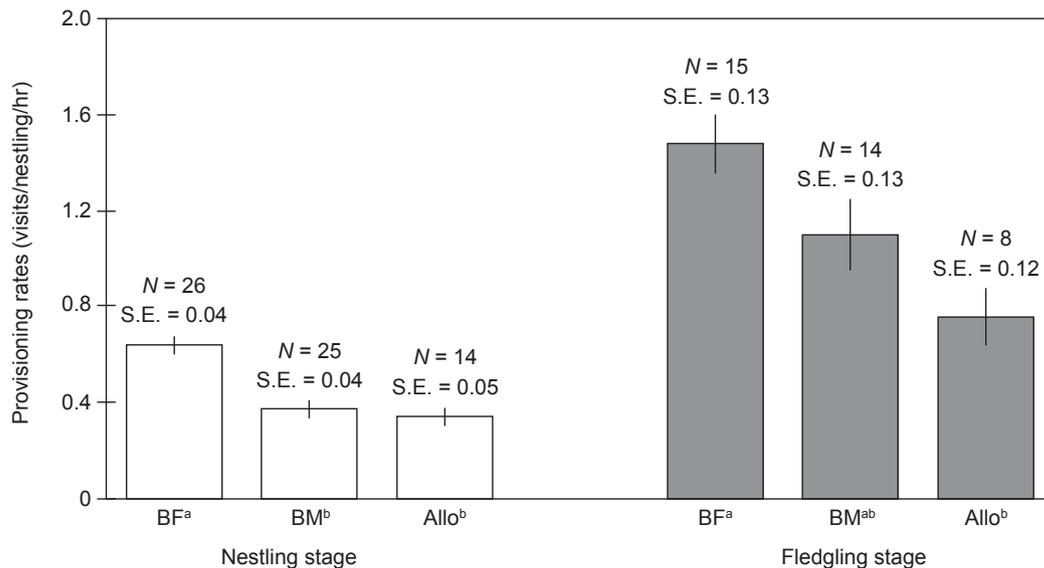


Fig. 3. Provisioning rates (visits/nestling/h) to the young by adults based on sex and breeding status within a group (BF, breeding female; BM, breeding male; and Allo, alloparents) during the nestling (ANOVA $F_{2,64} = 12.96$, $p < 0.001$) and fledgling stages (ANOVA $F_{2,37} = 5.59$, $p = 0.008$). Numbers above each bar refer to the number of nests observed and standard error. Breeding status followed by different superscript letter (^{a-b}) combinations within the same nest stage are significantly different (one-way ANOVA, Tukey multiple comparison, $p < 0.05$).

Table 3. Provisioning rates (visits/nestling/h) and the standard error (S.E.) of breeding females, breeding males, and alloparents from groups with different numbers of alloparents during the nestling stage

	No. of alloparents	S.E.	1 Alloparent	S.E.	2-5 Alloparents	S.E.
Breeder female	0.99 (6) ^a	0.09	0.77 (5) ^a	0.09	0.51 (17) ^b	0.07
Breeder male	0.60 (6) ^a	0.07	0.39 (4) ^a	0.12	0.31 (13) ^b	0.02
Alloparents			0.27 (4) ^a	0.08	0.37 (10) ^a	0.06
Total provisioning rate	1.65 (5) ^a	0.13	1.30 (5) ^b	0.85	1.21 (17) ^b	0.07

^{a,b}Numbers followed by different superscript letters within the same row significantly differ (one-way ANOVA, Tukey's multiple comparison, $p < 0.05$).

Provisioning rates of adults of different breeding statuses vs. group size

Provisioning rates of breeding females in groups with no alloparents were significantly greater than those in groups with 2-5 alloparents but not significantly greater than groups with 1 alloparent. Breeding males had the same trend where provisioning rates of males living in pairs were significantly greater than those in groups containing 2-5 alloparents. Rates for males living in pairs did not significantly differ from those in groups with 1 alloparent (Table 3). Interestingly, average provisioning rates of alloparents from single-alloparent groups did not significantly differ from the combined provisioning rates of alloparents from multiple-alloparent groups, (ANOVA $F_{1,13} = 0.866$, $p = 0.37$).

DISCUSSION

In our study, there was no significant correlation between territory quality and the number of alloparents, in contrast to previous studies on Pied Kingfishers, *Ceryle rudis*, (Reyer 1980, Reyer and Westerterp 1985), fairy-wrens, *Malurus cyaneus*, (Nias 1984, Nias and Ford 1992), and Laughing Kookaburra, *Dacelo novaeguineae*, (Legge 2000a). However, the trend of our data was consistent with that of Reyer (1980), in that pairs in poorer-quality habitats were more likely to accept unrelated alloparents than those in better-quality habitats. In our system, it is possible that the number of alloparents in a group is the result of reproductive success in the previous breeding season and recruitment of unrelated adults in the current breeding season, while habitat quality is highly ephemeral and difficult to precisely quantify due to the extremely dynamic and patchy nature of arthropod and fruit resources. Therefore, documenting clearer patterns would require much-larger samples of groups, perhaps incorporating multiple seasons of quality measurements.

There was also no significant correlation between reproductive success (measured by the number of fledglings produced) and habitat quality. In this dynamic system, it is possible that female quality in combination with the somewhat-random nature of predation may have partly or fully masked the effects of habitat quality. For example, as nesting success (8.8%) is typically low in this species in the study area (Pierce et al. unpubl. data), additional groups and habitat quality

data would be required to obtain better statistical power for this test. In addition, there was no correlation between the number of alloparents and reproductive success based on 3 yr of data. We found that the number of alloparents did not affect nesting success or provisioning rates in relation to habitat quality, indicating that alloparents might be more valuable in easing the workload on the breeders rather than increasing fledgling success. Alloparents did not reduce nestling mortality, and nest loss was mostly caused by large and potentially lethal predators (Pierce et al. 2007). Therefore, it is likely that Puff-throated Bulbuls are generally unable to discourage most approaching predators.

In cooperative breeding birds, other studies suggested that the number of alloparents affects nesting success through several possible mechanisms, one of which is provisioning rates to nestlings (Hunter 1985, Caffrey 1999, Legge 2000b, Kingma et al. 2010). Increased provisioning rates can increase nestling survival (Hunter 1985, Innes and Johnson 1996, Raihani et al. 2010), and a study by Caffrey (1999) suggested that alloparents may also allow shorter inter-brood times, such that more broods in a year can be produced, but we did not observe this. Komdeur (1994) compared the reproductive success between groups with alloparents and groups which had their alloparents experimentally removed. His experiments showed that the presence of 1 helper significantly improved the reproductive success of its breeding pair. Thus, it is possible that having alloparents allows for groups living in poorer-quality habitat to have equal levels of reproductive success to those in pairs (Reyer 1980). Although not statistically significant, our data suggested a similar trend with more alloparents in territories with lower food abundance.

Alloparents of Puff-throated Bulbul clearly reduced the workload of the breeders as observed in other species (Brown et al. 1978, Porkert and Spinka 2004, Canestrari et al. 2007, Kingma et al. 2010). The investment strategy of breeders with alloparents is variable, but fundamentally, alloparents provide additional resources to the parents' offspring or reduce their workload, as we observed in our study, or a combination of both (Hatchwell 1999). Meade et al. (2010) found that male breeders of the Long-tailed Tit, *Aegithalos caudatus*, reduced their feeding rates when alloparents were present at large broods and tended to reduce their feeding rates more than did females. However, we did not detect this in the

Puff-throated Bulbul, for which the proportional reduction appeared to be similar between the sexes. Herein, breeding females had significantly higher provisioning rates than breeding males or alloparents, but breeding males did not have significantly different provisioning rates to nestlings or to young fledglings compared to the alloparents. While studies have shown that the presence of alloparents can reduce breeder mortality (Khan and Walters 2002, Russell et al. 2007), a short-term study (3 yr) on the same population of Puff-throated Bubluls did not show a similar reduction (Sankamethawee et al. 2011).

We also observed notable variations in the level of provisioning among alloparents ranging from those which never or hardly ever provisioned, to those which provisioned as much as the breeders. It is possible that the "lazy" alloparents are tolerated because they act as insurance in case of the loss of 1 or more other group members (Baglione et al. 2010).

Having 1 or more alloparents in a group clearly reduced the workload of breeding Puff-throated Bulbul adults, but the benefit for the alloparents remains unclear. In several studies of helping behavior in cooperative breeding species, alloparents gain direct or indirect fitness depending on their degree of genetic relatedness to the breeding pair or nestlings. Our current data suggest that alloparents did not increase the reproductive success of the breeders or survival of nestlings; however, such benefits may be relatively subtle and therefore only become apparent over the course of several years of study or with much-larger samples of groups. Direct fitness for alloparents such as increased mating opportunities (Berg 2005), increased survival probability (Khan and Walters 2002), or improved parenting skills (Komdeur 1996, Cockburn 1998, Clutton-Brock 2002, McGowan et al. 2003) is still possible. Longer-term study of the survival and reproductive success of alloparents both related and unrelated to the breeding parents could elucidate the relative benefits of this cooperative breeding system for alloparents.

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